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NOTES ON THE IDENTIFICATION OF SUB-POPULATIONS OF FISH BY SEROLOGICAL AND BIOCHEMICAL METHODS, THE STATUS OF TECHNIQUES AND PROBLEMS OF THEIR FUTURE APPLICATION

by

B.B. Parrish

FISHERIES DIVISION, BIOLOGY BRANCH
FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1964

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General

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by

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Reviews concept of racial investigations, serological methods, and biochemical studies. Discusses future requirements in racial studies and makes comments, conclusions and recommendations concerning their use.

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1. INTRODUCTION

For a long time "racial" [1/] investigations have formed a prominent part of fishery research programs. They stemmed from Heinke's classical work at the end of the last century on the variations in morphological characters of herring (Clupea harengus L.). His and subsequent investigations showed that the north-east Atlantic herring population could not be treated as a single, homogeneous, biological unit, but, instead, was divided into a number of more or less well defined "tribes", "races" or "stocks", each with its characteristic ecological and dynamic properties, and subject to different amounts and kinds of exploitation.

This pioneer work provided the impetus for the development of intensive studies of the biological "characters" of exploited species throughout their range of distribution. A further impetus, and better defined objectives were also provided by the growth of theoretical population studies of exploited fish resources and the development of more rigorous quantitative methods of fishery assessment. This led to the formulation of the concept of the "unit stock" as the "basic" population subdivision in fishery assessment work. Various definitions of this unit, differing mainly in their biological completeness and precision have been given by a number of authors, expert working groups, etc. However, for the present purpose the formulation of the concept, made at the joint ICNAF/ICES/FAO Scientific Workshop in Lisbon in 1957 [2/] is used to define its main features. These are as follows:-

> '... a unit stock may be considered as a relatively homogeneous and self-contained population, whose losses by emigration and accessions by immigration, if any, are negligible in relation to the rates of growth and mortality...'

It is clear that the range of possible biological situations satisfying this definition is very wide and varies greatly for different species of fish. For some species, for example, the total population of a species constitutes a single unit stock and can be treated as a whole for fishery assessment and management purposes (i.e. for these of course the need for racial investigations does not arise). Indeed, in some situations the populations of two or more quite different species or groups of species or even genera, inhabiting the same general locality and having about the same population parameters, may be treated together as a single unit stock.

1/ The term "racial" investigations is used in this note in a wide, general sense, as a generic term to cover the whole range of investigations concerning the identification of population sub-divisions. No specific taxonomic significance is implied.

2/ A fuller discussion of this concept is given in the Proceedings of the Joint Scientific Meeting of ICNAF/ICES/FAO. It is also discussed at length in "Contributions to the Study of Subpopulations of Fishes", U.S. Fish and Wildlife Serv. Sp. Sci. Repts Fish. No.208, 1957, and in "Identification of Populations" by R. Muzinic in "Proceedings of the World Scientific Meeting on the Biology of Sardines and related species" 1960 Vol.III, pp.1287-1305, FAO, Rome.

However, for most species distinct population subdivisions (unit stocks) exist, which need to be treated separately for many if not all fishery assessment and management purposes as in the herring example referred to above. In general, such groups fall into the following two main categories:-

(a) Geographically isolated groups which are prevented from mixing freely and interbreeding with members of neighbouring groups by migration barriers.

(b) Reproductively isolated groups, inhabiting the same general locality, which occur and are exploited together during part (or all) of their life cycles, and which possess different vital statistics.

The first of these categories are sometimes very well defined ecologically, as when, for example, a demersal species is split into stocks on oceanic banks, separated from one another by depth or "water type" barriers. The second category however presents greater difficulties, especially amongst some of the pelagic species (e.g. herrings, sardines, tunas, mackerels and salmonids), the populations of which are known to be subdivided into "stocks", but the distributions of each of which often overlap during a large part of their lives, and between the members of which there are no easily recognisable morphological differences. Much of the work done in this field has been concerned with such species. Despite the large research effort devoted hitherto to these studies in, for example, the Atlantic herring, there is still much uncertainty about population subdivision. Indeed much of the current uncertainty about recent declines in certain North Sea herring fisheries stems from the lack of a clear understanding of the identities, interrelations and rates of mixing of different regional spawning groups within the North Sea population. "Racial" investigations therefore remain one of the main focal points of research into the population, biology and dynamics of this and other important species. It is in this sort of important context that the examination of new techniques must be viewed.

2. METHODS OF INVESTIGATION

The methods of investigation mostly used in "racial" studies hitherto fall into the following two main categories:-

(a) "Direct" studies of the distribution, movements, age and size composition, ecology and dynamics of the population throughout its range (e.g. tagging, experimental and exploratory fishing, egg and larval surveys, etc.).

(b) "Indirect" studies of the differences between measurable morphological and physiological characters of individuals within the population.

Following Heinke's work, much attention was paid to the differences between morphological characters (e.g. numbers of vertebrae, gill-rakers, fin rays and keeled scales; body proportions, differences in skeletal structures, etc.), and a large part of the research effort applied hitherto has been directed to their study, together with easily measurable physiological characters (e.g. growth and maturation). Much progress has been made, using this approach, in identifying major subdivisions within, for example, the north-east Atlantic herring, the Pacific sardine and the North Atlantic cod populations, which has fully justified the approach. However, with these and other species it has failed to provide sufficiently clear evidence of further possible subdivisions within each of the major ones, or of the rates of mixing of individuals of different groups outside the spawning season and their interbreeding rates (if any). The reasons for this stem largely from the fact that:

(a) The statistical distributions of most of the characters of different sub-groups within a population are very similar. Therefore, it is seldom possible for them to be used as labels for individual fish and analyses of them have to be made, statistically, on large samples.

(b) Most of the morphological and physiological characters exhibit plasticity under the influence of environmental factors, and their values may therefore differ significantly between year classes, or local groups within an otherwise homogeneous stock.

(c) Because of their environmental plasticity, no obvious genetic or evolutionary significance, and hence permanence, can usually be attached to the observed differences between the group values.

For these and other reasons some fishery biologists have recently turned their attention to the search for new characters and methods which are known from work on other animal groups to be more closely linked with the genotype and less subject to phenotypic variations. Amongst those which have received special attention are serology and the biochemistry of certain of the body substances, especially the blood proteins. Both of these kinds of investigations have been pursued extensively in anthropological, medical and genetic studies in man and other higher vertebrates, and an elaborate methodology has been developed for them.

2.1 Serological Methods

The methods adopted in these studies on fish have followed the "standard" techniques used in human and other higher vertebrate blood-group studies. Species which have been investigated, and for which published data are available include:-

(1) tuna[1/] (Cushing 1956; Suzuki, Shimizu and Morio 1958)
(2) Atlantic herring (Sindermann 1958; Sindermann and Mairs 1959)
(3) Pacific salmon (Ridgeway and Klontz 1960; Ridgeway, Cushing and Durall 1961)
(4) Sebastes (O'Rourke 1961; Sindermann 1961)
(5) spiny dogfish (Sindermann and Mairs 1961)

Blood-group studies have also been made of a number of freshwater species and of whales (Fujino 1953, 1958; Fujino and Cushing 1959).

(6) cod and other gadoids (O'Rourke 1959, Halversen and Möller 1961)

The application, by these workers, of a wide range of detailed techniques including isoagglutination, isoimmunisation and antiserum absorption and precipitation have produced positive evidence of the presence in fish of erythrocyte antigen systems and in some species also of naturally occurring haemagglutinins, as in the higher vertebrates. While for some species (e.g. gadoids) the investigations have so far proceeded little further than this exploratory stage, for others (e.g. tuna, herring and spiny dogfish) tentative, simple blood antigen systems have been worked out, which appear, as in the higher vertebrates, to be determined genetically, possibly in association with one or two genes. The possible future value of serological methods in investigating the identification of subpopulations, and in determining their distributions, interrelations and rates of mixing is therefore already clearly established, which indicates that they must be given serious consideration in the planning of future programs of "racial" work.

2.2 Biochemical Studies

As with serology, the use has recently been made of various biochemical

1/ Another paper entitled "Studies of the Erythrocyte antigens of albacore, bigeye, skipjack and yellowfin tunas, and their use in subpopulation identification", by Sprague, Holloway and Nakashima, was presented to the FAO World Scientific Meeting on the biology of Tunas and related species, held at La Jolla in July 1962. This paper was not available to me at the time of writing.

techniques, developed mainly in medical, physiological and genetics research, in taxonomic and "racial" investigations of some fish species. These have consisted mostly of application of chromatographic or electrophoretic methods to various proteinaceous body tissues and fluids, but especially of the blood (both serum and erythrocytes).

Results of such studies have shown marked and persistent differences between the chromatographic or electrophoretic patterns of these substances between recognized species of fish (see, e.g. Buzzati-Traverso and Rechnitzer 1953), which establishes their usefulness in general taxonomic work, but, of greater importance to the present enquiry, differences in these patterns have also been observed within the populations of some species. For example, Dannevig (1956) obtained distinct paper chromatographic patterns of muscle fluids of cod from different localities along the Norwegian coast; O'Rourke (1961) and Schaefer (1961) established differences between the chromatographic patterns of the gill mucus and muscle fluids respectively of the "marinus" and "mentella" types of the Oceanic redfish (Sebastes), while Sick (1961) has found differences between the agar-gel electrophoretic patterns of the erythrocyte to haemoglobins of cod and whiting from different areas.

Again, therefore, as with serological methods, work done so far has established the possible potentialities of these sorts of techniques in "racial" investigations of fish, and indicates the need for them being given serious consideration in future programs of work, either as alternatives, or in addition to serological methods or the "standard" methods used hitherto.

3. FUTURE REQUIREMENTS

As the literature shows, the use of serological and biochemical methods in "racial" investigations is very recent, and it is not surprising therefore that at present it is not clear to what extent results from their application will prove more advantageous than the older ones in assisting in the identification and delimitation of "unit stocks", or in the choice of the best species technique to use for a particular species. However, the work done so far with both methods has demonstrated clearly that serious attention must be paid to them in the future. This need has been recognized by various international scientific meetings and symposia in recent years, and a number of comments, conclusions and recommendations concerning their future use has been made. The following are some of these:-

(a) ICES Special Scientific Meeting on Herring "Races", Copenhagen, 1956

'... The following research items are considered to warrant special attention by herring workers...(ii) Studies of the genetical constitution of herring groups. It is recognized that this work presents formidable problems, but attention is drawn to the proposal made by Professor A.C. Hardy in his address to the special meeting of the Herring Committee in Edinburgh in 1949[1]/ to the need for a special European centre of research into the genetics of fish.'

(b) ICES/ICNAF Redfish Symposium, Copenhagen 1959

'... Several suggestions for future work seem in order:-
(a) ...
(b) In view of the potential value of biochemical and serological methods for studying systematics and populations of fish, these methods should be encouraged in the analyses of redfish populations of the North Atlantic. There are several ways in which they could be assisted by ICES and ICNAF.

1/ In Rapp.Proc.Verb., Vol.128, 1951

(i) By encouraging senior University staff biochemists and serologists with grants in aid and summer employment at fisheries laboratories.

(ii) By arranging for the preparation and publication of a handbook describing various methods used.

(iii) By encouraging government employment of serologists and biochemists in fisheries laboratories.

(iv) By arranging a world wide meeting, possibly in conjunction with the forthcoming FAO conference on fish physiology, of those working with serological and biochemical approaches to fish taxonomy.

(v) It is further recommended that certain biochemical determinations be accomplished at sea on freshly caught individuals...'

(c) FAO World Scientific Meeting on the Biology of Sardines and Related Species, Rome 1959

... It is hoped that those attempting to identify and determine the structure of population units will continue to explore the possibilities of other techniques that will constitute powerful new tools (e.g. serology...).'

(d) FAO World Scientific Meeting on the Biology of Tunas and Related Species, La Jolla 1962

'2.5 Blood Groups

Through studies of blood groups, with standard immunological techniques, it is possible to determine whether or not several samples represent a single sub-population or a mixture. Blood groups are under genetic control, and it was noted that geneticists believe sub-population differences must have developed over periods of the order of centuries rather than decades.

Difficulties in the use of this technique concern collection and transportation of samples. ...there is much variability in this regard among species. For example, skipjack must be bled within two or three hours of death, whereas yellowfin and bigeye can be bled after several days, provided they have been iced, not frozen. These latter similarly withstood shipment better than skipjack.

While results of experiments so far have been most gratifying, there obviously remains far more to do than has been done. The need for world-wide coordination recurred in comment, as did the need for standardized terminology. Both of these topics were subject for resolutions at the 1961 Hawaii Conference[1] (on Pacific Tuna biology) which called for the establishment of a center in Honolulu to aid in the exchange of blood samples and reagents, and in standardizing terminology. A modest start has been made in implementing these resolutions.'

1/ The report and resolutions of this Conference were not available to me at time of writing.

'5. Suggested Resolutions

(1) The Meeting should support resolution 2 of the Pacific Tuna Biology Conference ... with respect to a center for blood samples and reagents, modified as seems appropriate in the light of findings of the Working Group, which it is anticipated will be designed to consider this problem during the Meeting. It should urge implementation of recommendation 8 of that conference with respect to improved methods for the transport and storage of blood samples, and the utilization of wide ranging tuna fleets to collect such samples.

(2).....

(3) The Meeting should urge all nations concerned to attack the many problems raised with all possible vigour, using not only the established means of tagging and serology, but seeking out new approaches and drawing on techniques developed in other disciplines, which may be fruitful.

(4) The Meeting should encourage such programmes as:

(a) ..., (b) augmented studies of blood group systems in yellowfin, skipjack, albacore and other species throughout the Pacific ...'

It is clear from these various conclusions and recommendations that serological and biochemical studies have already become well established in some fishery research centres and for some species (especially serological studies on tuna in the Pacific). However, it is also clear that in other areas and species, these approaches have either not yet begun or are in a very early, exploratory stage.

A feature of these techniques is that they are not usually the stock in trade of most biologists employed at fishery biology institutes; they require the specialist training of geneticists, physiologists or biochemists. Fishery research institutes all over the world are not therefore confronted simply with the problem whether to begin such studies, but also whether to fill their all too few staffing vacancies with recruits skilled in these specialist roles. Many have undoubtedly not yet done so (perhaps rightly) through lack of sufficient, easily appraisable information on the real potential advantages of these methods over the conventional ones. For example, in few of the published papers so far, have the results been compared with those obtained with other methods (Sindermann (1959), mentions the similarity between his serological results for herring and those obtained from parasitological studies). Such comparisons undoubtedly have been or are being made for several species at the present time (e.g. Danish haemoglobin electrophoretic studies of Baltic cod are being done in conjunction with tagging experiments, and Scottish herring ones with other characters (meristic otolith types, fecundity, etc.). Only when these have been clearly displayed will it be possible to determine objectively the relative merits of the new and the older techniques.

Within this new range of methods (i.e., serological and biochemical) there is a choice of specific techniques, most of which have been applied by one worker or another to some species of fish. It would be extremely valuable, for those, as yet uncommitted, to have at their disposal as comprehensive an appraisal as possible of the technological procedures (including the collection and storage of material), speed with which observations can be made, their suitability for field operations, special facility requirements (instruments, etc.) and their cost (see recommendation (ii) of ICNAF/ICES Redfish symposium), to assist in the choice of technique. In this context it is interesting that in the North American tuna and salmon work, serological techniques have been mostly (if not exclusively) used, whereas the Danish whiting and cod investigations (Sick, 1961) have been confined to biochemical studies (agar-gel electrophoresis) of erythrocyte haemoglobins. What factors governed these different choices?

One of the advantages claimed for these methods is that differences between immunological characters, and at least some of the biochemical ones (e.g. haemoglobin

types) are that they are genotypic and largely unaffected by environmental influences.[1/] This is obviously of importance in taxonomic studies and simplifies the interpretation of results, but it may not necessarily be of overriding importance for "unit stock" identification, unless all population subdivisions, satisfying this concept and meaningful as separate "management units" have diverged sufficiently to produce differences in the genotype. This may, in fact be so, but far too little is known of the genetics and rates of speciation in fish to judge it objectively at the present time.

The problem of population subdivision in fish is of such importance in many applied fisheries investigations, and the application of the new techniques of serology and biochemistry of body proteinaceous substances sufficiently far advanced for steps to be taken, on a world wide basis, to bring together all available expert knowledge on their methodology and applicability in the fisheries field. This, I think, could be sponsored appropriately by FAO as part of its biological program. The objectives, as I visualize them would be best achieved by (a) the appointment of expert consultants in these technical fields to prepare detailed descriptions of the techniques, (b) the bringing together of a small expert group, consisting of fishery biologists, familiar with "racial" problems in different species of fish, and experts in the serological, biochemical, genetics and taxonomic fields (including particular specialists concerned with animal groups other than fish), to review and discuss the application of these specialist techniques (and perhaps others) in investigating the problem of population sub-division (i.e. sub-specific groups).

1/ This claim is based mainly on the evidence gained from investigations of the higher vertebrates, but there is some supporting evidence that this is also the case for fish. However, more direct information on possible environmental influences in fish is required, especially for the biochemical properties.

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